Acoustic identification of bats in the Arava desert (rift valley)

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Modern advances in acoustic technology have made possible new and broad ranges of research in bioacoustics, particularly with regard to echolocating bats. In the present study we present an acoustic guide to the calls of 15 species of bats in the Arava (rift valley), Israel, with a focus on their bioacoustics, habitat use and explaining differences between similar species. We also describe a potential case of frequency separation where four bat species using six call types appear to separate the frequencies of their calls to minimise overlap. The studied community of bat species is also found in other Middle Eastern deserts including the deserts of Jordan, Syria and Saudi Arabia and we hope that data gathered will benefit other bat researchers in the region.

Key Words: Insectivorous desert bats; echolocation; acoustic separation

Introduction

The ability to determine the activity and richness of species in a given area is essential to assess habitats and ecosystems. Many echolocating bats have species specific calls and are relatively easy to monitor acoustically (Fenton and Bell 1981). Combined with the ecosystem services they provide (Kunz et al. 2011), this makes them ideal bioindicators for habitat assessment (Jones et al. 2009, Russo and Jones 2015).

Bat species' echolocation calls can be divided broadly into two temporal categories: high duty cycle (HDC) and low duty cycle (LDC). HDC calls are longer in duration and have a shorter inter pulse interval resulting in the majority of a sequence being occupied by the call of the bat, thus a higher duty cycle. Conversely, LDC calls are short in duration and have long inter pulse intervals, because the bat calls and waits to listen for the returning echo, resulting in longer periods of silence (Fenton 1999). Calls can also be defined by shape. Constant frequency (CF) calls have a typically large portion of the call with no change in frequency and are synonymous with HDC calls. Narrowband calls have little change in frequency over time and are sometimes called quasi-constant frequency (QCF). Conversely, frequency modulated (FM) calls are broadband and sweep through a range of frequencies in a short period of time. Narrowband calls are best suited to detection in open space foraging while broadband calls are better for localising an object and tend to be used more by gleaning bats (Neuweiler 1989, 1990, Jones and Rydell 2003, Schnitzler et al. 2003). Individual calls can contain components of multiple shapes; for instance a "hockey-stick" shaped call typical of Pipistrelles has a FM portion followed by a narrowband QCF component (Kalko and Schnitzler 1993, Russo and Jones 2002). Moreover, during a sequence of calls there may be distinct differences between search, detection, approach and attack phases of call sequence. A typical Pipistrelle bat will use a more QCF call during the search phase, then FM-QCF during

detection and approach, finally emitting a rapid "buzz" of FM calls with an increased call rate during the attack phase (Jones and Rydell 2003).

Identification of species is typically based on common parameters both temporal (e.g. call duration and inter pulse interval) and spectral (e.g. start, end and peak frequency) as well as the overall frequency modulation pattern (FM, CF, QCF) of the call. However, individual species do not always use just one fixed call type. An individual will alter its call in different habitats and with changing distance to obstacles (Kalko and Schnitzler 1993, Bartonicka and Rehak 2005) as well as depending on whether there are other bats nearby (Obrist 1995, Ratcliffe et al. 2004, Ulanovsky et al. 2004, Gillam et al. 2007, Bates et al. 2008, Amichai et al. 2015). Some species show age and sex differences within the population as well as distinct changes due to the individual calling (Masters et al. 1995), while populations of the same species in different global regions may have different call structures (Thomas et al. 1987, Murray et al. 2001). Finally, some species have such similar calls that identifying the calls from one another becomes less reliable (Barclay 1999).

Because acoustic monitoring is a passive technique that does not require continuous user input and does not interfere with the normal activity of the study animal, most modern systems can be set before dusk and left recording unattended until dawn. This tends to result in very large data sets with minimal collection effort. However, manually identifying the species in such large sets of recordings can be time consuming, particularly at sites with high activity and diversity. As a result of this there have been attempts to automate the process. Automatic call identification falls into three categories: analysis that is based on predefined echolocation call parameters both spectral and temporal (Vaughan et al. 1997, Parsons and Jones 2000, Obrist et al. 2004, Basil et al. 2014), using automated speech recognition (Skowronski and Harris 2006) and machine learning tools where a computer program is trained on a library of calls and then uses learned parameters to classify future calls. In the

case of the latter tactic there are currently three methods in use: artificial neural networks (ANN) (Parsons and Jones 2000, Parsons 2001, Jennings et al. 2008, Walters et al. 2012) , classification trees (Adams et al. 2010) or automated speech recognition (Skowronski and Harris 2006).

In the deserts of the Middle East there has been only one comprehensive study on the identification of the bat species in the region. Benda (2008) produced an acoustic key for bats in the Sinai, but it is based on few individuals from each species; with five species only being recorded once. Benda et al. (2010) provide a description of echolocation calls for species of bats found in Jordan. Dietz and von Helversen (2004) produced a morphological key with a description of echolocation calls for bats in Europe. This relies on caught bats and all recorded calls are from the hand, and the description of calls is only based on end frequency and a rough shape of the call; no spectrograms are presented to aid in acoustic identification. More recently, Walters et al. (2012) produced an automatic identification system for the bats of Europe based on a large library of calls. Both of these keys do not include many species found in the Middle East.

In this paper we present a guide to the acoustic identification based on predefined echolocation call parameters of all insectivorous bat species in the Arava desert in Israel. We aim to clarify distinctions between similar/easily misidentified species. We also provide the parameters to an automatic identification system and discuss the acoustic separation of the frequency range by the QCF bats in the region.

Methods

During the spring and summers of 2008-2010 we recorded bat echolocation calls in the Arava rift valley between the Dead Sea and the Red Sea in Israel (30º45N 35º15E) using a BatCorder automatic acoustic monitoring device (EcoObs, Nuremberg, Germany @ 500 kHz and 16 bit). The BatCorder is a direct recording system that provides full spectral and temporal information for all calls in real time, yielding accurate acoustic data. We hung this device from a tree 1-2 m from the ground, and at sites where no trees were suitable, from a 1m-high stand. Once set the BatCorder can be left unattended, recording until retrieved, automatically triggering to record upon detection of a bat call, and continuing to record until 800 ms after the triggering event. The recordings were made in both natural desert sites and man-made villages or date palm fields.

Automatic identification parameters

We initially analysed calls from 2008 manually to identify bats in the region and create a call library using SasLab Pro v. 4.40 (Avisoft Bioacoustics, Berlin, Germany). Recorded calls were identified to species initially from published acoustic identification guides (Dietz and von Helversen 2004, Benda et al. 2008, Dietz et al. 2009). We manually deleted the echoes and any noise, and used the automatic measurements feature to calculate start frequency, end frequency, peak frequency, call duration and inter-pulse interval.

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We then selected peak frequency at the start, end and at the maximum amplitude of the call as parameters for automatic identification using the automatic measurements feature of SasLab Pro to classify the calls in each file. We omitted call duration and interval from this process as the frequent overlap of the call with its echo meant it was too error-prone. Using axis-parallel thresholds we set a range of values for each parameter based on the extracted frequencies; if a call adhered to all the variables it was identified as the defined species. We then expanded the defined range of the frequencies for each species until all typical search

125 calls from the library were identified, including any calls with echo overlap. Additional bat
126 species' calls that had not been originally recorded in 2008 (which would have been marked
127 as unidentified) were identified manually. The calls of at least five passes (typically the first
128 five recordings) were added to the library and used for automatic identification classification
129 and the rest were used to test the defined set of identification parameters.

130 There are specific limitations to this approach. As catching bats in the hand was often not
131 possible due to the open nature of the study area, most calls in the library are from free flying
132 bats. However, the known differences in the acoustic parameters of calls of bat species found
133 in the region (Dietz and von Helversen 2004, Ulanovsky et al. 2004, Holderied et al. 2005,
134 Berger-Tal et al. 2007, Bayefshy-Anand et al. 2008, Benda et al. 2008, Dietz et al. 2009,
135 Benda et al. 2010) allowed a reasonable assumption of positive identification of all passes in
136 the library.

137 ***Bat pass analysis***

138 As with all acoustic monitoring there are drawbacks to relying on calls to measure bat
139 activity. There is a strong species specific bias against whispering bats as louder bats will be
140 recorded over greater distances than quieter ones (Adams et al. 2012), and we could not
141 correct for that bias in this study. Acoustic monitoring also does not provide an accurate
142 estimate of the number of individuals in a region. While it is possible to identify recordings
143 containing calls from one single individual from temporal or spectral differences, there is no
144 way to reliably estimate the exact number when two or more individuals are flying together.
145 Moreover, there is no way to distinguish one bat flying back and forth through a monitored
146 area from multiple individuals foraging together. For this reason, we tested automatic species
147 identification performance on passes rather than individual calls.

148 ***Similar species and manual confirmation***

149 The frequency of *Rhinopoma hardwickii* and *Rhinopoma microphyllum* calls overlap slightly.
150 From looking at the call library and literature (Dietz and von Helversen 2004, Levin et al.
151 2007, Dietz et al. 2009), we selected a cut-off frequency of 30.2 kHz to differentiate between
152 the two species. To confirm this cut-off we needed a large sample size of both species so we
153 selected all recordings from 2009 that had only one individual of either species (1,125
154 passes), extracted the end frequency of all calls, and created a frequency histogram of the
155 mean end frequency for each pass. On the frequency histogram there are four peaks (Figure
156 3A). Based on the evidence for anatomical sexual dimorphism in the genus *Rhinopoma*
157 (Levin et al. 2013) as well as differences in call peak frequency (Levin 2005) we interpreted
158 these as the gender specific peaks of call distribution of the two species. We classified the
159 two peaks with lower frequency as the larger species, *R. microphyllum*, and the other two
160 peaks as *R. hardwickii.* The midpoint between the two central peaks is at 30.2 kHz which
161 corroborates our decision to use this as the cut-off frequency between the two species.

162 *Pipistrellus rueppellii* and *Hypsugo bodenheimeri* overlap slightly in all call parameters;
163 however until 2010 no calls with an end frequency over 50 kHz were recorded. Moreover, *H.*
164 *bodenheimeri* was one of the most commonly recorded species both acoustically and in mist
165 nets, while *P. rueppellii* was never captured in the hand. Therefore we assumed that *P.*
166 *rueppellii* was not present until 2010 and unless the end frequency was over 50 kHz we could
167 not reliably identify an individual as *P. rueppellii*. Hence, calls were considered to be *H.*
168 *bodenheimeri* when the end frequency was below 50 kHz and only marked as *P. rueppellii*
169 when above this threshold.

170 *Otonycteris hemprichii* and *Plecotus christii* overlap in all used parameters so distinction
171 between them had to be made manually. We did this based on the overlap of the call and the
172 harmonic combined with the ratio of call duration and end frequency. While doing so we
173 extracted the end frequency and duration of all the calls without the echoes. We calculated

the mean value for each pass and used discriminate function analysis (DFA) to determine the ability of these variables in determining the difference between the two species; it was able to separate 98.6% of the passes accurately (Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 5. Spectrograms of Pipistrelle-type bat calls. A: *Pipistrellus rueppellii*, B: *Hypsugo bodenheimeri*, C: *Pipistrellus kuhlii* D: *Eptesicus bottae* and E: *Tadarida teniotis*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87.

Figure 6. Spectrogram of *Barbastella leucomelas* alternating between the two call types. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 7. Spectrograms of bats with a *Plecotus*-type call. A: *Otonycteris hemprichii*, B: *Plecotus christii* and C: *Nycteris thebaica*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure ~~Figure 8~~). All other species were different enough from any other species that no further alterations to the defined frequency ranges were necessary.

When establishing the frequency ranges for the automatic parameters, errors typically occurred in two cases. Noise (e.g. wind, footsteps) was occasionally identified as bats that call at lower frequencies (below 25 kHz: *O. hemprichii*, *P. christii*, and *Tadarida teniotis*). To reduce this error we looked at all files that were marked as any of these bat species to ensure that they were indeed bat passes. This is also the point at which we differentiated *O. hemprichii* and *P. christii*. Because three common species had an approximate end frequency of 30 kHz (*Eptesicus bottae*, *R. hardwickii*, and *R. microphyllum*), occasional calls in a pass were sometimes misidentified. Hence, we manually confirmed the automatic identification

when two or fewer of these bats were identified in a file. Additionally, in order not to miss new bat species we manually checked files where no bat was identified in a file. The number of files that had to be manually confirmed varied depending on the amount of noise that triggered the BatCorder, but typically it was less than 10%.

Data analysis

Due to variability of bat calls within a pass, we were only interested in identifying the whole pass of an individual as a guide of activity levels and not all individual calls. We defined a pass as ending after 800 ms of silence or at the end of a file. We therefore tested the identification success as correctly identifying all bat passes, or all the bats present in a file and not all individual calls.

We compared the automatic identification to human classification on three days (total of 722 passes) from 2008 that had not been used to create the library. Compared to manual identification the automatic identification was correct in 95.39±0.76% passes. Errors were predominantly due to missing quiet calls that were below the analysis threshold, rather than due to misclassification as another species. To examine the frequency division in the *Rhinopoma*-type species we plotted a fast fourier transform (FFT) of one call from both sexes of *Rhinopoma* species as well as both species of *Taphozous* present in desert regions of Israel: *T. nudiventris* and *T. perforatus* (Yom-tov et al. 1992, Korine and Pinshow 2004).

We used the R-2.13.2 statistical environment (The R Foundation for Statistical Computing, 2008) for all statistical tests and graphs. We manually deleted echoes and noise and created all spectrogram figures in SasLab Pro (v4.4, Avisoft Bioacoustics, Berlin, Germany).

Results

Identified bats

Over the three years we recorded 15 species of insectivorous bats in the area from five families (**Error! Reference source not found.**~~Figure 1~~). In total we recorded 27,053 bat passes over 160 nights usually recording at two sites a night. 119 passes were marked as unidentified bats that needed to be added to the library.

Rhinopoma-type (QCF) calls

We recorded three species of bats with narrow bandwidth calls: *T. nudiventris*, *R. hardwickii* and *R. microphyllum*, although *T. nudiventris* was only recorded in 2010. All three species of bats produce multi-harmonic calls with anywhere between 1 and 5 harmonics detectable and the most energy in the second harmonic (**Error! Reference source not found.**~~Figure 2~~).

T. nudiventris typically calls with the second harmonic at 22-25 kHz, *R. hardwickii* with the second harmonic at 32-35 kHz, and *R. microphyllum* with the second harmonic at 27-31 kHz; however, there is overlap between the latter two (**Error! Reference source not found.**~~Table 1~~). Both *R. hardwickii* and *R. microphyllum* appear to show sexual dimorphism in the frequency of the calls as expected for this genus (Levin 2005). The presumed female calls 2 kHz higher than the male of the same species and a further 2 kHz difference between the presumed male *R. hardwickii* and female *R. microphyllum* (as indicated by the arrows in **Error! Reference source not found.**~~Figure 3~~A).

CF (HDC) calls

We recorded three species of bats that have FM aspects of the call at either ends with a CF component in the middle, the latter making up the bulk of the call: *Asellia tridens*, *Rhinolophus hipposideros* and *R. clivosus*. All three species have one dominant harmonic (the 2nd) and show high-duty cycle call behaviour (**Error! Reference source not found.**~~Figure 4~~).These

species are easily separated by the CF frequency. *A. tridens* has echolocation calls with the CF component of the call at around 118 kHz, *R. hipposideros* around108 kHz and *R. clivosus* at approximately 85 kHz (**Error! Reference source not found.**~~Table 1~~).

Pipistrellus-type calls

We recorded five species of bats with an FM-QCF call shape typical of Pipistrelle bats: *P. rueppellii, H. bodenheimeri, Pipistrellus kuhlii, Eptesicus bottae* and *T. teniotis* (**Error! Reference source not found.**~~Figure 5~~) which typically have one dominant fundamental frequency; but, depending on the loudness of the call, often the 2nd and occasionally 3rd harmonic is discernible. The five species are distinguishable primarily through their end frequency: *P. rueppellii* typically has an end frequency of 50-53 kHz; *H. bodenheimeri* 45-47 kHz; *P. kuhlii* 38-41 kHz; *E. bottae* 29-31 kHz; and *T. teniotis* 14-16 kHz (**Error! Reference source not found.**~~Table 1~~).

Barbastella leucomelas

B. leucomelas is unique among the recorded bats as it alternates between two call types (Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 5. Spectrograms of Pipistrelle-type bat calls. A: *Pipistrellus rueppellii*, B: *Hypsugo bodenheimeri*, C: *Pipistrellus kuhlii* D: *Eptesicus bottae* and E: *Tadarida teniotis*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87.

Figure ~~Figure 6~~). Type I is a short (1.81±0.11 s), FM call often with 2 harmonics detectable, similar to the calls emitted by the FM bats (below). The call sweeps from 36 kHz to 30 kHz. Type II is an easily identifiable and unique FM convex curved call that starts at 42 kHz and ends at 32

kHz. Only type II was used for automatic identification because type I overlapped with *E. bottae* a much more commonly recorded bat.

Plecotus-type calls

We recorded three species of bats with FM calls typical of *Plecotus* species: *O. hemprichii*, *P. christii* and *Nycteris thebaica* (Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

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Figure 6. Spectrogram of *Barbastella leucomelas* alternating between the two call types. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure ~~Figure 7~~). The calls of all three species are multi-harmonic, but *O. hemprichii* and *P. christii* have two discernible harmonics with the most energy in the 1st harmonic while *N. thebaica* has two or more harmonics with either approximately equal energy across the 5th and 6th harmonic or most energy in the 5th; the first 4 harmonics are not discernible. The echolocation call of *N. thebaica* is very short in duration (1.35±0.13 s) and the dominant harmonic sweeps down from 78 kHz to 63 kHz (**Error! Reference source not found.**~~Table 1~~). Because it was only recorded once and has equal energy across two broadband harmonics, the automatic measurements of *N. thebaica* were too variable to be identified automatically; however the calls would have been marked as unidentified and therefore identified manually.

Otonycteris hemprichii has a short broadband call with an end frequency of between 18 kHz and 22 kHz; the duration of its call tends to longer and more variable than *P. christii* which

has a typically shorter and higher frequency call with an end frequency of between 21 kHz and 25 kHz (**Error! Reference source not found.**~~Table 2~~), thus these species of bats overlap in call frequency parameters. We distinguished them manually through the ratio of the end frequency to duration of the call, with *O. hemprichii* typically emitting calls greater than 3 ms and less than 22 kHz while *P. christii* called for less than 2 ms and above 22 kHz (Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

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Figure ~~Figure 8~~). We also distinguished them in the spectrogram where there is a significant overlap of the 1st and 2nd harmonics in *O. hemprichii* while *P. christii* showed very little if any overlap (Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

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Figure ~~Figure 7~~A and B).

Discussion

The validity of the automatic acoustic identification depends on the number and quality of the calls recorded, as well as the variability of the calls of each species. The *Rhinopoma spp.* were both numerous and have relatively consistent calls between passes. While the two species overlap in call parameters, the cut-off frequency of 30.2 kHz falls at the half-way point between the histogram peaks of the presumed female *R. microphyllum* and the male *R. hardwickii.* It is highly likely that some passes were misclassified, but only in the minority of cases. *T. nudiventris* while not as common in the study area as the other two species has calls that do not vary extensively so we are confident in the identification of its passes.

Likewise, the HDC bats were not recorded extensively, but all species in the region have unique species-specific calls. Hence, the identification of these calls is reliable. Conversely, the bats with *Pipistrellus*-type calls were typically common. However, they vary aspects of their calls considerably with changes in habitat, prey type and over the course of an attack sequence (Kalko and Schnitzler 1993). To combat this latter variability, we aimed to identify passes as a whole, and typically within a sequence the majority of calls were in the search phase. Thus the overall pass was reliably identified. With the exception of *P. rueppellii* and

H. bodenheimeri there was no overlap in the calls of these bats (*P. kuhlii*, *E. bottae*, *T. teniotis*) so the identification of these species is robust. It is possible that some of the *H. bodenheimeri* passes are actually *P. rueppellii* but as *H. bodenheimeri* was recorded consistently over the three years and is so much more prevalent in the region (Yom-tov et al. 1992, Hackett et al. 2013, Korine et al. 2015), it is unlikely to be a common misidentification. Alternatively, *P. rueppellii* was overlooked for two years, but as it was only in 2010 that calls over 50 kHz were first recorded it is more likely that it was absent prior to this.

The rarer bats such as *B. leucomelas* and *N. thebaica* have unmistakable calls, but the library is based on only one pass/individual. *N. thebaica* was not included in the automatic identification and *B. leucomelas* was identified only four more times. It is to be assumed that these species are substantially underrepresented because of their low call amplitudes, but were unambiguously identified, either manually (*N. thebaica*) or automatically (*B. leucomelas*). Since there is no other bat call similar to either, we are confident of the classification. Similarly, the slightly more common whispering bats *O. hemprichii* and *P. christii* were checked manually and distinguished from one another in the spectrogram after being identified automatically as a group.

The call parameters we present here are in line with those previously reported. Benda et al. (2008) described the echolocation calls of *R. hardwickii* (identified as the subspecies *R. cystops*), *R. clivosus*, *R. hipposideros*, *A. tridens*, *E. bottae*, *H. bodenheimeri* (identified by the authors as a conspecific of *H. ariel*), *O. hemprichii*, *P. christii* and *T. teniotis*. Three species' descriptions were from solitary individuals. As *R. microphyllum* was not recorded in the Sinai, Benda does not discuss the difference between the two *Rhinopoma* species. *O. hemprichii* was recorded only once and *P. christii* was recorded three times and only in the hand or upon release. Likewise, *P. rueppellii* was not recorded in the Sinai so distinctions

between that and *H. bodenheimeri* were not described. Other species (e.g. *B. leucomelas* and *N. thebaica*) have not been described in such detail in the region before.

In general, the automatic identification allows for a reliable and efficient processing of the large data sets recorded during acoustic monitoring. Manually checking files where errors in the automatic identification are most likely and separating similar calls manually significantly decreases the likelihood of misclassification, but it will never be possible to gain a 100% identification rate even manually.

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Identified bats

We recorded and identified 15 species of insectivorous bats in the Arava rift valley; *T. perforatus* is the only desert-dwelling insectivorous bat species in Israel that was absent. These species occupy a wide range of ecological niches hunting different prey and utilizing varying foraging tactics in a range of habitats.

Occasionally hunting in groups *R. hardwickii*, the Lesser Mouse-Tailed Bat, forages in open habitats (Feldman et al. 2000) mostly on Coleoptera (Whitaker and Yom-Tov 2002). They have a characteristic gliding flight that uses the updrafts common near cliff edges (Habersetzer 1981). *R. microphyllum*, the Greater Mouse Tailed Bat, feed mostly on Coleoptera and ants at height above vegetation and over water (Sharifi and Hemmati 2002, Whitaker and Yom-Tov 2002, Korine and Pinshow 2004, Levin et al. 2009). *T. nudiventris*, the Naked-Rumped Tomb Bat, mostly prey on Coleoptera and fly high in open areas (Yom-Tov 1993, Korine and Pinshow 2004, Whitaker and Karatas 2009). *Asellia tridens*, the Trident Leaf-nosed Bat forages in a vegetation-rich, cluttered environment, catching Coleoptera, Heteroptera, Diptera and Lepidoptera flying close to vegetation (Jones et al. 1993, Feldman et al. 2000, Dietz et al. 2009, Amichai et al. 2013). *R. hipposideros*, the Lesser Horseshoe Bat, forages typically by aerial-hawking with agile flight often in dense

vegetation, but is also able to glean insects from vegetation (Jones and Rayner 1989, Feldman et al. 2000, Bontadina et al. 2002, Korine and Pinshow 2004, Zahn et al. 2008, Dietz et al. 2009). They feed mainly on Lepidoptera, Diptera, Hymenoptera and Neuroptera (Arlettaz et al. 2000, Feldman et al. 2000). *R. clivosus*, Geoffroy's Horseshoe Bat, has been reported either as specialising on Coleoptera (Feldman et al. 2000)or as more of a generalist (Whitaker et al. 1994, Benda et al. 2010) and typically forages in a cluttered environment (Feldman et al. 2000, Korine and Pinshow 2004).

P. kuhlii, Kuhl's Pipistrelle, is an aerial-hawker that typically forages in urban areas or over water and in edge spaces, predominantly on Diptera, Hymenoptera and Coleoptera. They are attracted to villages by artificial lighting and are likely to only be in the area as a result of these villages (Feldman et al. 2000, Korine and Pinshow 2004). *P. rueppellii*, Rüppell's Pipistrelle Bat, also feeds mostly on Diptera, Coleoptera and small Lepidoptera through aerial-hawking and is typically recorded over water and in edge spaces (Whitaker et al. 1994, Feldman et al. 2000). *H. bodenheimeri* forages in edge spaces of cliffs and vegetation. It is a generalist aerial-hawker feeding on Lepidoptera, Trichoptera, Coleoptera, Diptera, Hymenoptera and Homoptera (Whitaker et al. 1994, Feldman et al. 2000, Riskin 2001, Korine and Pinshow 2004). *E. bottae*, Botta's Serotine Bat, are generalists that prey predominantly on Coleoptera and Hymenoptera, but depending on the season will also take Hemiptera, Diptera and Orthoptera; it typically forages at the edges of cliffs and vegetation (Feldman et al. 2000, Korine and Pinshow 2004, Holderied et al. 2005, Dietz et al. 2009). *T. teniotis*, European Free-tailed Bat, is a fast flier (65km/h) that aerial-hawks high above the ground (10-300m) allowing a broad range of habitats away from most obstacles (Bayefshy-Anand et al. 2008, Dietz et al. 2009). They predominantly feed on Lepidoptera, but will opportunistically take Diptera, Coleoptera, Neuroptera and Hymenoptera (Rydell and Arlettaz 1994).

406 Almost nothing is known about the foraging behaviour and diet of *B. leucomelas*, Eastern
407 Barbastelle Bat, and it is rarely recorded in the region. The closely related *B. barbastellus* is a
408 specialist preying upon eared moths which it catches by low-amplitude stealth hawking
409 (Goerlitz et al. 2010). *O. hemprichii*¸ Hemprich's Long-eared Bat, are passive gleaners that
410 rely on prey generated acoustic cues (e.g. rustling sounds) of non-aerial arthropods such as
411 Coleoptera and Arachnids. They typically fly close to the ground (40-100 cm) land for 2-5
412 sec to catch prey which they consume while in a slow, gliding and widely circling flight 3-7
413 m above the ground (Arlettaz et al. 1995, Holderied et al. 2011). Little is known about *P.*
414 *christii*, Lappet-eared Bat, with regard to foraging behaviour as it is a recently isolated
415 species (Spitzenberger et al. 2006). However, Feldman et al. (2000) noted that *P. austriacus*
416 foraging in a location now known to have only *P. christii* and not *P. austriacus* were
417 Lepidopteran specialists. Finally *N. thebaica*, Egyptian Slit-faced Bat, is a generalist and
418 opportunistic feeder preying upon Lepidoptera, Coleoptera, Diptera, Hymenoptera and
419 Hemiptera primarily in open savannah woodland areas (Gray et al. 1999). It is a gleaning
420 bat, that can hunt during continuous flight or from perches whereby it listens for prey while
421 hanging from a roost, then directs its head toward the sound and rapidly moves its ears back
422 and forth before attacking (Fenton et al. 1983, Gray et al. 1999).

423 ***Frequency separation***

424 The separation of frequencies evident in the FFT of the QCF bats provides an interesting
425 insight into the acoustic niche separation of a group of bats (**Error! Reference source not**
426 **found.**~~Figure 3~~B). The apparent sexual dimorphism of the calls in the two recorded *Rhinopoma spp.*
427 results in the peak frequencies of the dominant harmonic being spread evenly with 2 kHz
428 between them. Interestingly when *T. nudiventris* is included, the 3rd harmonic of its call falls
429 between the presumed male and female of *R. hardwickii*; this is not the dominant harmonic
430 but often also contains a substantial amount of energy. *T. perforatus*, not recorded in the

Arava, but common in the adjacent Negev desert (Korine and Pinshow 2004) and around the Dead Sea (Yom-Tov 1993) similarly has its dominant harmonic between the presumed male and female *R. microphyllum*. Between the four species and six call types, the peak frequencies in the relatively narrow range of 26-34 kHz appear to be divided with apparently little conflict. It is important to note that this is a representation based on just one call from each individual. The situation is likely to be more complicated when considered at the community level where there will be greater intraspecific variation.

Frequency separation has been examined before, but predominantly with regard to Rhinolophid species, and in the tropics where bat communities can consist of 50 species (Heller and Helversen 1989, Kingston et al. 2000, Kingston and Rossiter 2004, Thabah et al. 2006). Yet there is still debate within the field. For instance, Heller and Helversen (1989) described a frequency separation among 12 species of bats in Malaysia that was more evenly distributed than expected by chance. However, when Kingston et al. (2000) returned to the same site they were unable to replicate the results. Interestingly, the frequency separation that we present is opposite to Kingston and Rossiter's (2004) findings in two of the three morphs of *Rhinolophus philippinensis*. They describe "harmonic hopping" in the bats' echolocation calls where the calls of different morphs of the species occur at different frequencies. The CF components of the calls line up such that the 2nd (dominant) harmonic of the large morph corresponds to the 1st harmonic of the small morph; the 4th and 2nd harmonics likewise line up. Conversely, the harmonics of the intermediate morph fall in between the harmonics of the other two morphs, similar to our findings of frequency separation.

This division of the frequency range is potentially a form of character displacement, and may serve to deepen our understanding of geographic changes in species' echolocation calls. In the absence of a species with a similar call type and frequency, another species would potentially be able to exploit a wider range of frequencies or perhaps even shift. Indeed,

Russo et al. (2007) found that *R. hipposideros* and *R. euryale* emitted calls with higher and lower frequencies, respectively, when flying with *R. mehelyi*. Since *R. mehelyi* calls in between *R. hipposideros* and *R. euryale* the authors concluded that this shift was a character displacement in order to avoid overlapping frequencies and aid in species recognition.

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Figure Legends

Figure 1. Representative echolocation call from each of the 15 species of insectivorous bats recorded in the Arava. *T.n.*: *Taphozous nudiventris*, *R.h.*: *Rhinopoma hardwickii*, *R.m.*: *Rhinopoma microphyllum*, *N.t.*: *Nycteris thebaica*, *A.t.*: *Asellia tridens*, *Rh.c.*: *Rhinolophus clivosus*, *Rh.h.*: *Rhinolophus hipposideros*, *P.r.*: *Pipistrellus rueppellii*, *H.b.*: *Hypsugo bodenheimeri*, *P.k.*: *Pipistrellus kuhlii*, *E.b.*: *Eptesicus bottae*, *B.l.*: *Barbastella leucomelas*, *Pl.c.*: *Plecotus christii*, *O.h.*: *Otonycteris hemprichii*, *Ta.t.*: *Tadarida teniotis*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%.

Figure 2. Spectrograms of bats with narrow bandwidth *Rhinopoma*-type calls. A: *Taphozous nudiventris*, B: *Rhinopoma hardwickii* and C: *Rhinopoma microphyllum*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%.

Figure 3. A: Frequency histogram of the mean call end frequencies of *Rhinopoma hardwickii* and *Rhinopoma microphyllum.* Black arrows indicate peaks on the histogram that correspond to the frequencies (from left to right) for *R. microphyllum* presumed male and female and *R. hardwickii* presumed male and female. B: Exemplary power spectra for all narrow bandwidth bats found in the Negev and the Arava, Israel. *Taphozous perforatus* in the Arava, but it is included here as the ranges are likely to overlap.

Figure 4. Spectrograms of HDC bats. A: *Asellia tridens*, B: *Rhinolophus hipposideros* and C: *Rhinolophus clivosus*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 5. Spectrograms of Pipistrelle-type bat calls. A: *Pipistrellus rueppellii*, B: *Hypsugo bodenheimeri*, C: *Pipistrellus kuhlii* D: *Eptesicus bottae* and E: *Tadarida teniotis*. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87.

Figure 6. Spectrogram of *Barbastella leucomelas* alternating between the two call types. Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 7. Spectrograms of bats with a *Plecotus*-type call. A: *Otonycteris hemprichii*, B: *Plecotus christii* and C: *Nycteris thebaica.* Spectrogram parameters: FFT length 512, Hamming window, overlap 96.87%

Figure 8. Scatterplot of the mean end frequency and mean duration for each individual *Otonycteris hemprichii* and *Plecotus christii* pass.